Sucrose avoidance by American robins (*Turdus migratorius*): implications for control of bird damage in fruit crops

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Abstract   Altering the relative sugar content in fruit is a potential alternative to chemical, aural and visual repellents to control bird damage to cultivated fruit crops. Some frugivorous birds, such as the American robin (*Turdus migratorius*), lack the digestive enzyme sucrase, and therefore cannot digest sucrose. It was predicted that robins would avoid consumption of foods that contain sucrose. When offered sweetened agar cubes that contained glucose, fructose, sucrose, or a hexose mixture, total consumption was significantly lower and faecal sugar concentration higher in the sucrose tests. In tests involving two sugars, mean total consumption was reduced when sucrose was eaten. Development of high-sucrose fruits warrants further investigation as a means to mitigate bird damage to certain fruit crops.

Keywords   American robin; aversion; bird damage; fruits; North America; sucrose intolerance; sugar preferences; *Turdus migratorius*

Introduction

North American producers of small fruits, such as blueberries, cherries and grapes, suffer extensive, economically significant crop losses to migratory birds (Mott and Stone, 1973; Stone, 1973; Crase *et al.*, 1976). For example, losses to birds can reach 20–75% in early-ripening blueberry crops in Florida (Nelms, Avery and Decker, 1990) and can exceed 40% in cherry orchards in New York and Ontario (Brown, 1974). Bird damage to blueberries and cherries is expected to increase substantially in the United States because of recent expiration of the registration of methiocarb, an effective bird-repellent chemical. The lack of a chemical control agent limits the options for bird control in fruit crops (Tobin and Dolbeer, 1987).

Modifying the relative sugar content in fruit through conventional breeding or bioengineering is a potential alternative to current techniques for reduction of bird damage. Some fruit-eating bird pests, such as American robins (*Turdus migratorius*), lack the digestive enzyme sucrase which hydrolyses the disaccharide sucrose to its constituent monosaccharides, fructose and glucose (Karasov and Levey, 1990). Unhydrolysed sucrose cannot be transported across the intestinal epithelium and hence is of no nutritional value. Thus, if sucrase-deficient birds consume sucrose, digestive problems such as osmotic imbalance and diarrhoea may ensue, and an aversion to the food item may develop (Martínez del Rio and Stevens, 1989). For example, the European starling (*Sturnus vulgaris*) lacks sucrase, as do other members of the avian families Sturnidae (starlings, mynas), Mimidae (thrashers, mockingbirds), and Muscicapidae (true thrushes, old world flycatchers) that have been examined (Martínez del Rio, 1990). In a previous study, starlings preferred fructose and glucose solutions, but rejected sucrose solutions (Schuler, 1983). Sucrose aversion was correlated with sucrase deficiency, and was elicited in one-day tests in which 0.7 M sucrose (24% sucrose by weight) solutions were paired with distilled water. Furthermore, in 2-day trials 0.175 M (6% sucrose) solutions elicited aversions (Martínez del Rio *et al.*, 1988).

Because American robins lack sucrase, we predicted that they would not be able to digest sucrose-containing foods. We also predicted that, like starlings, robins would accept glucose and fructose, but reject sucrose. We examined these predictions by performing choice tests with the three sugars that are naturally found in fruits – fructose, glucose, and sucrose – using red agar cubes as artificial fruits.

Materials and methods

Subjects

Wild adult American robins were mist netted in late January 1990, in Marion County, Florida. The birds were marked with numbered aluminium leg bands and weighed while free of digesta within 4 h of capture. Birds were held in small groups (4–8 individuals) and housed in wire mesh cages ($1.8 \times 1.2 \times 1.2$ m) in a covered outdoor aviary. During the first 2 weeks of acclimatization to captivity, robins were fed *ad libitum* a mixed diet of mealworms

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(*Tenebrio* spp.), banana mash [a 10% sugar maintenance diet for frugivorous birds (Denslow *et al.*, 1987)], and holly berries (*Ilex* spp.). We believed that the wild robins had been primarily eating insects because they were captured from a wet prairie where no fruits were available. Thus, a mixed diet of insects and fruits was necessary to assist in digestive adaptation to the maintenance frugivore diet (Levey and Karasov, 1989). Following 2 weeks of the mixed insect–fruit diet, the birds were fed banana mash *ad libitum* daily with supplements of mealworms offered once per week.

In the third week of captivity, 10 robins were taken from the group holding cages and housed individually in test cages ($0.46 \times 0.46 \times 0.92$ m). They were allowed 2 weeks for acclimatization to the smaller cages before testing. The birds then were trained for 1 week to consume agar cubes containing a 1 : 1 mixture of glucose plus fructose (15%). Throughout the period of captivity, digesta-free body mass of each individual was recorded weekly at dawn.

Initial mean ($\pm$ s.d.) body mass of the 10 birds was 75 (± 2) g. Body mass of individuals varied little throughout the period of testing, indicating that the birds remained in good health, with a coefficient of variation < 3% for all individuals.

Artificial fruits

Sugars were offered in agar cubes (~ 0.125 cm^3) at a concentration of 15% (g sugar/100 ml solution, Bolten *et al.*, 1979). Anhydrous β-D-[$-$]-fructose, D-glucose, or sucrose (150 g) was mixed with boiling water (1 litre) and purified plant cell agar (10 g). Chemicals were obtained from Sigma Chemical Co. (St Louis, MO). The solution was coloured with French's red food colouring (2 ml or 1 ml). Because the robins frequently dropped cubes from one bowl into another, we colour-coded the cubes in two shades of red. The two colours had Munsell values of 7.5R 4.0/15.0 (red) and 6.25R 5.0/14.0 (pink) (Smithe, 1974).

Choice tests

Birds ate the maintenance banana mash *ad libitum* from dawn until 0745 h each morning (~ 75 min). Then the banana mash was removed and they were deprived of food for 1 h before each test. The individually caged robins were offered two clear plastic cups (8.5 cm diameter, 3 cm deep), each containing ~ 30 g of the test cubes. The cups were bound together with a rubber band and placed at the bottom front of the cage to reduce the possibility of biases due to preferences for a particular side of the cage. Water was provided *ad libitum* throughout each trial.

Placement of sugar types (right versus left) was randomized among birds independently with a coin toss before each test. Sugar colour was fixed within a given trial, such that all birds received one sugar in red cubes and the other sugar in pink cubes. Aluminium trays were placed under each cage to catch dropped cubes and faeces. After each 3 h trial, dropped cubes were counted and replaced in their respective cups, which were then reweighed. Consumption was estimated by the difference between the

initial and final cup plus food masses, corrected for evaporation of water. Evaporative loss was estimated with two pairs of cups containing the same types of sugar cubes tested in each trial and exposed to the same conditions as the test cubes.

Two series of two-choice tests were performed, closely following the methodology of Martínez del Rio, Karasov and Levey (1989) for sugar preferences in cedar waxwings (*Bombycilla cedrorum*). Series 1 tested the ability of robins to discriminate between agar cubes that lacked or contained sugar. Four trials were performed with each of 10 birds on 4 consecutive days with agar cubes that lacked sugar ('plain' cubes) and cubes that contained one of the test sugars. Sugars were tested in the order: a 1 : 1 mixture of glucose : fructose, glucose, sucrose, then fructose. Two birds per trial were videotaped and the number of pecks directed at each food cup and the water container were noted from each day's film. Series 2 tested for preferences between sugars by offering birds all possible pairwise combinations of the four sugar groups. Each bird was offered each of the six pairs of sugars on consecutive days.

Two additional tests were performed: the first was a test for colour preference by robins for red or pink, using only glucose cubes; the second was a test of preference for glucose cubes versus a 1 : 2 mixture of sucrose and glucose to see if the presence of sucrose affected consumption.

The series 1 test of the hexose mixture versus plain cubes lasted 1.5 h; all other experiments lasted 3 h. The sugar concentrations [% (g solute per 100 ml solution)] of three faecal samples per bird were determined with a refractometer (± 0.25%) in all series 1 trials and in the series 2 trials that involved sucrose.

Statistics

A preference ratio for each bird that consumed any artificial fruit was calculated for each pair of foods by dividing the consumption of each food by total consumption (Kare, Black and Allison, 1957). Mean preference ratios ($\pm$ s.d.) were calculated for each experiment. A preference for a sugar is determined if the preference ratio is > 0.5; indifference, if the preference ratio $= 0.5$; and rejection, if the preference ratio is < 0.5 (Kare *et al.*, 1957). A t test with arcsin, square root-transformed preference values was used to test the null hypothesis that there was no difference between the mean sugar preference value and 0.5 for each experiment of the series 1 tests. A one-way repeated-measures ANOVA was used to test the null hypothesis that there were no differences of mean consumption and faecal sugar concentrations among sugar treatments. It was assumed that there were no carry-over effects of sugar type in order to apply the ANOVA. As a conservative method to separate selected means, t tests, were used (Wilkinson, 1989).

Results

Series 1

Total consumption ranged from 0 to 25.3 g per bird among experiments that tested for preferences of plain or sugar

Table 1. Mean (±s.d) total consumption, percentage faecal sugar, and sugar preference ratios for robins in two-choice tests between agar cubes with or without sugar(s)

Test sugar	n	Total consumption (g per bird)		Percentage faecal sugar		Sugar preference ratio	
		$\bar{x}$	(s.d.)	$\bar{x}$	(s.d.)	$\bar{x}$	(s.d.)
Glucose + fructose	6	10.9	(6.2) a[a]	3.6	(0.7)	0.81	(0.23)*[b]
Glucose	6	17.9	(6.1)	3.6	(1.6)	0.94	(0.09)**
Fructose	6	11.8	(8.0)	3.5	(1.6) a	0.66	(0.46)
Sucrose	6	4.5	(5.5) b	11.5	(2.3) b	0.85	(0.15)**

[a]Different letters within the same column indicate significant differences in values as determined by ANOVA and t tests, [b]asterisks in the right-hand column indicate significant differences between mean preference ratios and 0.5 as determined by one-tailed t tests ($*p < 0.05$; $**p < 0.01$)
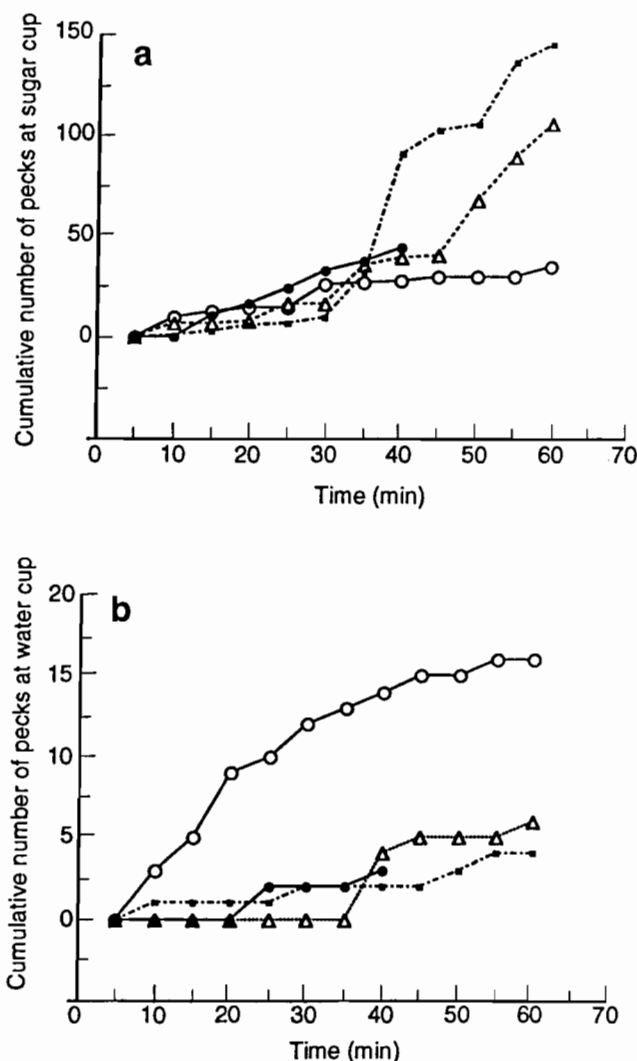

Figure 1. Cumulative number of pecks into cups per 5 min interval by one American robin during the first 60 min of series 1 tests for the sugars sucrose (○), fructose (■), glucose (△), and 1:1 glucose:fructose (●). a, Pecks into the sugar cups; b, pecks into the water cup

cubes. Mean consumption per experiment ranged from 4.5 (±5.5) to 17.9 (±6.1) g per bird and was lowest when sucrose was tested (Table 1). The mean concentration of sugar in the faeces ranged from 3.5% (±1.6) to 11.5% (±2.3) and was highest when sucrose was offered (Table 1).

High faecal sugar of those birds that consumed sucrose indicates an inability of the digestive tract to absorb the sugar. Mean sugar preference ratios ranged from 0.66 (±0.46) to 0.94 (±0.09) and was lowest when fructose was tested. Robins preferred sugar cubes that contained glucose, the hexose mixture, or sucrose over plain cubes.

Robins on videotape repeatedly sampled plain and sugar cubes by picking up and splitting or mashing them. A typical pattern was to peck rapidly several times in one cup, followed by repeated pecks in the other cup. After 30–40 min of alternate sampling, the peck rate for monosaccharide sugar cubes increased dramatically, whereas that for the disaccharide, sucrose, remained low (Figure 1). In addition, the only videotaped bird that consumed a large amount of sucrose showed an increase in number of pecks at the water container when consuming sucrose, suggesting increased water consumption (Figure 1).

Series 2

American robins preferred the mixed hexoses over glucose or sucrose, and glucose over sucrose (Table 2). No preferences were expressed when fructose was tested. Faecal sugar concentration was negatively related to preference for hexoses over sucrose (Figure 2). Across all trials, preference for sucrose was negatively correlated with total consumption (Figure 3). In the test for colour preferences, mean total consumption was 21.4 (±4.7) g. There was no preference for cube colour ($\bar{x}_{RED} = 0.69 \pm 0.34$; $t = 1.71$, $p = 0.12$). In the test of preferences for a 1:2 mixture of sucrose and glucose versus glucose, mean total consumption was 17.9 (±4.0) g. There was no preference for a sugar type ($\bar{x}_{SG} = 0.40 \pm 0.30$; $t = 1.04$; $p = 0.33$).

Discussion

Food choice by birds is affected by pre- and postingestional cues. Preingestional cues of foods include colour, location, smell, flavour and texture. Many frugivores have distinct colour preferences, such as red over blue, green, and yellow (McPherson, 1988). These preferences may be learned at a very young age in a process of food imprinting (Hess, 1964), or may be contingent on other associated traits of the foods (Willson, Graff and Whelan, 1990). Colour was offered at two levels and no differences were found in

Table 2. Mean preference ratios (± s.d.) and sample size for test sugars eaten by American robins

	Paired sugar								
	Glucose			Fructose			Sucrose		
Test sugar	$\bar{x}$	(s.d.)	n	$\bar{x}$	(s.d.)	n	$\bar{x}$	(s.d.)	n
Glucose + fructose	0.65	(0.18)	9[*a]	0.61	(0.23)	8	0.70	(0.16)	9[**]
Glucose				0.44	(0.26)	10	0.69	(0.24)	10[*]
Fructose							0.59	(0.17)	8

[a]Asterisks indicate significant differences between mean preference ratios and 0.5 as determined by one-tailed t tests ($*p < 0.05$; $**p < 0.01$)
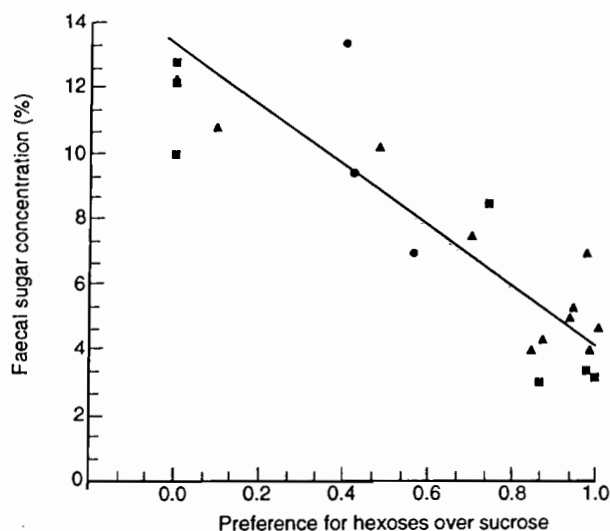

Figure 2. Mean faecal sugar concentration (%) of American robins in relation to preference ratios for hexoses vs. sucrose for the sugars fructose (■), glucose (▲) and 1:1 glucose:fructose (●). $y = 13.77 - 9.70x$, $R = 0.85$, $p < 0.01$
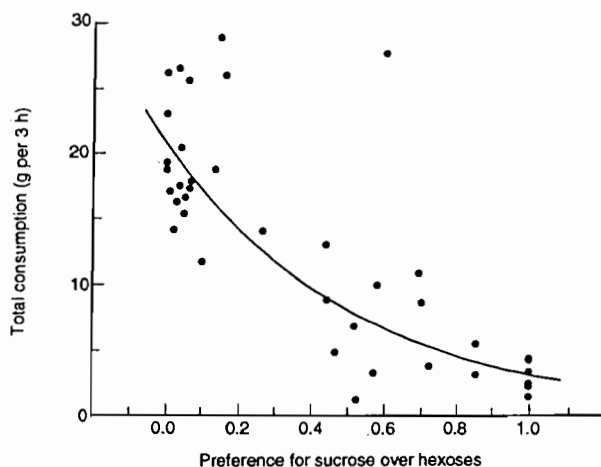

Figure 3. Preference ratios of American robins for sucrose vs. hexoses in relation to total consumption (g per 3 h). $y = 20.85 \times 10^{(-0.83x)}$; $R = 0.82$, $p < 0.01$

choice of red or pink cubes by robins; thus, it was concluded that a bias for shades of red did not affect food choice. However, future research should examine whether the coupling of other colour cues will influence food choice

or have a training effect, teaching robins to identify specific foods.

Sugar flavour could affect food choice by robins, if they can distinguish the tastes of fructose, glucose and sucrose, as do several tropical fruit-eating birds (Levey, 1987). Robins demonstrated a preference for sweet versus plain artificial fruits if the fruits contained glucose alone, a mixture of glucose plus fructose, or sucrose, but not if they contained fructose alone. Fructose tastes > 50% sweeter than glucose to humans (Moskowitz, 1974) and is slowly metabolized by birds (Hazelwood, 1986). If robins detect the flavour of fructose, then they might adjust intake of this apparently energy-poor food. With the exception of the fructose trial, the results reported here are comparable to those for European starlings (Martínez del Rio et al., 1988) and cedar waxwings (Martínez del Rio et al., 1989). These species showed a clear preference for each sugar type over a plain solution or plain artificial fruit.

Postingestional cues of foods include glycaemic response, osmotic homoeostasis, neural irritation, and satiety. The lack of sucrase in robins that consumed sucrose may have caused several negative postingestional effects. Consumption of sucrose by sucrose-intolerant animals elicits intestinal discomfort, lack of increase in blood sugar and osmotic imbalance (Dahlqvist, 1962). Approximately 50% of ingested sucrose remains undigested and appears intact in the faeces; the remainder may be acid-hydrolysed in the intestine to lactic and fatty acids (Dahlqvist, 1974). The intact disaccharide is too large to be absorbed. It acts osmotically to draw water into the intestine, thus causing cramps, bloating, and diarrhoea. Similar physiologically stressful responses may have occurred in robins that ate any sucrose, thus providing reinforcement for either fasting or sampling other artificial fruits.

When American robins ate sucrose, their total intake of artificial fruits declined. These results suggest that robins developed an aversion to sucrose in the short-term experiments. With repeated or long-term exposure to sucrose, the response could be similar to that of sucrose-intolerant starlings. Starlings develop a conditioned aversion to dilute (6%) sucrose solutions (Martínez del Rio et al., 1988). The present results are in contrast to those for cedar waxwings, which have the enzyme sucrase in the intestinal brush border and can digest sucrose, albeit inefficiently (Martínez del Rio et al., 1989). Total consumption of artificial fruits increased when sucrose was offered to waxwings.

Development of an aversion to sucrose explains the series 1 test where fructose-sweetened cubes were not
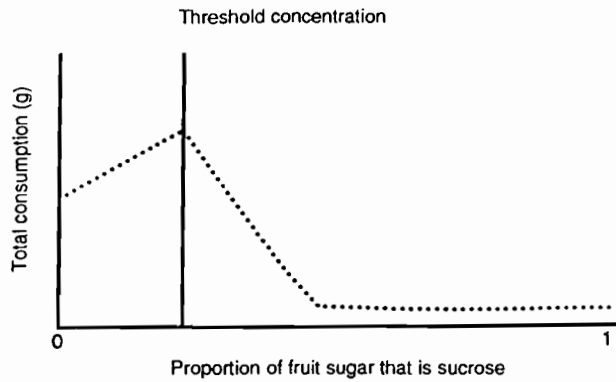
Threshold concentration

Figure 4. Proposed model for the relationship of total consumption (or total damage) of fruits by American robins or other sucrose-intolerant frugivores and relative proportion of fruit sugar that is sucrose

a threshold concentration of sucrose, it is predicted that consumption will decrease, owing to the postingestional effects described above. Determination of this threshold concentration is crucial to the development of high-sucrose fruits through traditional plant breeding or bioengineering methods. Further work is needed to identify the context(s) in which aversion can be ensured. The practicality of artificially selecting for high-sucrose fruits as special bird-deterrent strains will depend not only on commercial needs and the availability of sufficient genetic variability for diverse sugar production by these fruits, but on the predictability of avian food choice behaviour in the typical agricultural field where alternative foods are available.

Acknowledgements

preferred to plain agar cubes. The order of sugar testing probably influenced the robins' feeding responses. The hexose mixture was tested first, glucose second, sucrose third, and fructose last. A learned aversion to sweet-tasting cubes could have developed in these birds after their experience with sucrose, thus training them to avoid fructose in future tests.

Robins had no bias against the mixture of 1 : 2 sucrose and glucose when paired with pure glucose. This combination of sucrose and glucose was tested to explore the effects of sucrose in the presence of a hexose. Many fruits contain 10–15% sugars in solution and sucrose may comprise as much as one-third of the sugar content in some cultivars of small-berried fruits (Whiting, 1970). Additionally, 6% sucrose elicited an aversion in starlings. It was predicted that sucrose avoidance by robins tested with a sucrose concentration at this level might be attenuated by the presence of an easily metabolized hexose in the artificial fruit. Total consumption did not change, nor was a preference expressed by the robins. The results may be attributable to the availability of an alternative acceptable food source that allowed the robins to continue feeding at normal levels even when ingesting sucrose.

These results suggest several hypotheses concerning food choice by American robins and other fruit-eating birds that lack the digestive enzyme sucrase: (1) American robins can distinguish among the fruit sugars and will show a preference for fruits that contain glucose and/or a hexose mixture over sucrose in long-term feeding trials; (2) American robins will demonstrate preferences even when sugars are presented in mixtures that could be available in domestic fruit cultivars; and (3) there is a relationship of colour and conditioning to food choice by robins. Future research is planned to test these hypotheses.

In broad scope, it is hypothesized that there is a strong relationship between sucrose concentration in fruits and damage from robins or other frugivores that lack sucrase (*Figure 4*). At low concentrations of sucrose, total consumption is high and therefore total damage is great. At intermediate concentrations of sucrose, consumption may reach a peak as robins attempt to meet energy demands by eating more fruits that are only partially digestible. Beyond

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